THE NATURAL GROUPING OF THE BREMIDÆ (BOMBIDÆ) WITH SPECIAL REFERENCE TO BIOLOGICAL CHARACTERS.¹

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In the introductory pages of his rather negativistic treatise on the psychobiology of bumblebees, Wagner ('o6), after calling attention to the immense taxonomic importance of biological characters in the case of spiders, cites—by way of contrast several examples of the disconcerting polymorphism in the coloration and habits of bumblebees and comes to the following pessimistic conclusion:² "These are the facts which compel us from the very beginning to give up all hope of finding fixed and unalterable characters in the taxonomy of bumblebees for the elucidation of the biology of these insects, and *vice versa*, of deriving suitable data from their biology for taxonomic purposes."

As we shall see later, this statement of Wagner ('o6), as so many other of his assertions (cf. von Buttel-Reepen, 'o7, '14; Wheeler, '19; and Plath, '23b, '24), is based upon superficial observations and is wholly untenable. During the past fifty years, several important attempts, most of which antedate Wagner's ('o6) work, have been made to subdivide the Bremidæ into natural groups. These subdivisions have been based either upon (1) coloration, (2) structure, or (3) habits, and in some cases on two or all three of these.

In this paper the writer wishes to discuss in detail those attempts to subdivide the Bremidæ into natural groups which have been based primarily upon biological characters, and to sub-

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² "Dies sind die Tatsachen, welche uns von allem Anfange an zwingen, jede Hoffnung darauf aufzugeben, in der Systematik der Hummeln feste und unveränderliche Züge für die Aufklärung der Biologie dieser Insekten zu finden und umgekehrt aus dem biologischen Kriterium geeignete Angaben für die Systematik der selben... zu schöpfen."

ject these latter to a critical examination in the light of extensive biological observations on some of our American species. Before doing so, it seems desirable however to review briefly several efforts at grouping which have been made on the basis of (I) coloration and (2) structure.

GROUPING ON THE BASIS OF COLORATION.

The Austrian entomologist von Dalla Torre ('82) is apparently the only one who attempted to subdivide the Bremidæ on the basis of coloration. However, since many species of the genus *Bremus* (*Bombus*) which are not closely related show very striking similarities in coloration, *e.g.*, *Bremus americanorum*³ and *Bremus terricola*, this method of grouping is a very artificial one and for this reason has not been favorably received by other workers. In this connection the present writer would like to confess that he himself, not long ago (cf. Plath '22a, pp. 40–41), made a similar mistake with respect to the genus *Psithyrus*.

GROUPING ON THE BASIS OF STRUCTURE.

There have been several attempts made to group the Bremidæ on the basis of structure. The first of these was by the Russian General Radowszkowski ('84) who divided the genus *Bremus* into eleven groups. This scheme of grouping was later somewhat modified by Franklin ('12/'13) in his "Bombidæ of the New World," in which the then-known, eighty-five American species of the genus *Bremus* are divided into seven groups, a procedure which has been followed by other American workers. This method of grouping has been further extended by Franklin ('12/'13) to the American species of the genus *Psithyrus* which he divides into three groups.

Another scheme of grouping which has much in common with Radowszkowski's ('84) is that of Vogt ('11) who divides the genus *Bremus* into nine subgenera, which Ball ('14) and Krüger ('16 and '20) later increased to ten and thirteen respectively. The last-named author, in addition to making a few modifications in

³ Dr. Joseph Bequaert and the writer have recently studied De Geer's description and figure of *Bremus pennsylvanicus*, and, like Dr. T. H. Frison ('23), have come to the conclusion that it is better to use the name *americanorum* until the type specimen of De Geer is located.

the nine subgenera established by Vogt ('11), has divided the genus *Bremus* into two sections, on the basis of the presence or absence of a spinous projection on the posterior, distal angle of the metatarsus of the middle legs. This character may prove of considerable importance in determining the genetic relationship of the various species of bumblebees, since, as we shall see later, it seems to go hand in hand with certain fundamental differences in the method by which these insects feed their larvæ.

Another independent subdivision of the non-parasitic bumblebees on the basis of structure is that by Robertson ('03), who removed certain species from the genus *Bremus* (*Bombus*) and erected the genus *Bombias*, chiefly on the basis of the size and position of the ocelli. This innovation does not seem to have found favor with European workers, but *Bombias*, either as genus or subgenus, is in common use in the United States.

Among the attempts to divide the Bremidæ into natural groups on the basis of structure, we may also include that of Friese and von Wagner ('10), who constructed a "Stammbaum" which is intended to show the probable genetic relationship of the fifteen species of *Bremus* occurring in Germany. This scheme of grouping will, no doubt, have to be considerably modified, since it is not in harmony with certain fundamental biological and structural characters which have been pointed out by Sladen ('99 and 12) and Krüger ('16 and '20).

GROUPING ON THE BASIS OF HABITS.

The first one who used biological characters for subdividing the Bremidæ was the English entomologist Smith ('76). In the second edition of his "Catalogue of British Bees," he divides the English species of the genus *Bremus* into Surface-builders (Section I.) and Underground-builders (Section II.). While this method of subdividing the Bremidæ may be of some value to the amateur naturalist, it is of little importance for taxonomic purposes, since certain species of bumblebees, *e.g., Bremus vagans*, make use of many diverse nesting sites: underground, on the surface, in stone walls, hollow trees, birds' nests, attics, fur coats, etc.

A more promising and dependable biological character for

dividing the Bremidæ into natural groups was discovered by the late F. W. L. Sladen ('99) who called attention to the fact that the various English species of the genus *Bremus* employ two very distinct methods of feeding their larvæ. Since this short, but epoch-making paper of Sladen ('99) has been overlooked by several workers, and since it forms the chief basis for the present discussion, it seems advisable to quote the two following paragraphs from it.

"Taking nests of humble-bees and keeping them under observation in specially constructed hives has been a hobby of mine for some years, and it is astonishing what a quantity of interesting information one can gather in this way about the habits and life-history of the dozen or so species that have been recorded trom this country, several of which are very common and familiar to every one. It appears that each species has habits and proclivities more or less peculiar to itself, and these, if they could be accurately observed and recorded, would help very much in the systematic arrangement of the species, which in this interesting genus is unusually difficult, owing to the lack of easily recognisable structural differences, and to the little reliance that can be placed on colouring.

"As a result of taking a number of nests it appears that most of the *Bombi* found in this country may be separated into two groups, on what seems to be a rather important difference in the manner of raising their young. These groups may be conveniently named (I) the '*pouch-makers*' and (2) the '*pollen-storers*." The *pouch-makers* form little pockets or pouches of wax at the side of a wax-covered mass of growing larvæ, into which the workers drop the pellets of pollen direct from their hind tibiæ on the return to the nest from the fields. The *pollen-storers*, on the contrary, store the newly gathered pollen in waxen cells specially made for the purpose, or in old cocoons specially set apart to receive it, from which it is taken and given to the larvæ through the mouths of the nurse-bees as required."

Thirteen years later, Sladen ('12, pp. 40-44, 152-153), in addition to elaborating the foregoing plan in general, changed the term *Pouch-makers* to *Pocket makers*, and further subdivided the latter group into *Pollen-primers* and *Carder-bees*. However,

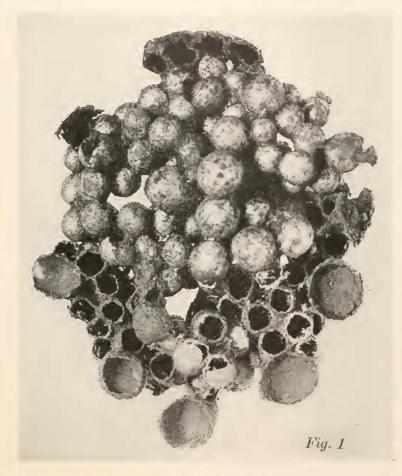
shortly after this revision had appeared in print, Sladen ('12, pp. 274–275) discovered that the character on the basis of which he had established the Pollen-primers is not a dependable one and hence inserted the following paragraph among his "Additional Notes": "B. latreillellus was considered to be a pollenprimer because pollen was found under the eggs in a nest in an advanced stage examined in 1911. But in a nest in an earlier stage kept under observation in 1912 the eggs were laid in cells that contained no pollen, although in at least one case pollen was put into the cell and removed before the eggs were laid. Should future investigation show that *latreillellus* is a pollen-primer only under abnormal conditions, a better name for the group, consisting or ruderatus, hortorum, latreillellus and distinguendus. would be 'Long-faced Humble-bees'; the term 'pollen-primers' could then be restricted to ruderatus and hortorum. Latreillellus and distinguendus are not closely related to ruderatus and hortorum."

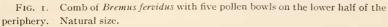
For several summers the present writer has devoted most of his time to the study of the biology of bumblebees, and has had occasion to examine the nests of about 200 *Bremus* colonies belonging to the following North American species: *affinis*, *americanorum*, *bimaculatus*, *fervidus*, *impatiens*, *perplexus*, *occidentalis*, *separatus*, *ternarius*, *terricola*, *and vagans*. This material furnished an excellent opportunity to test the soundness of Sladen's ('99 and '12) classification, as applied to four of our seven American groups. The results of this investigation show that Sladen's ('99 and '12) classification provides an excellent basis for further taxonomic and phylogenetic work, but that certain details of his scheme will have to be modified.

As already stated, Sladen ('12) divides the English Bremidæ into two main groups, the *Pollen-storers* and the *Pocket-makers*. In regard to the last-named group Sladen ('12, p. 44) says: 'When the usual receptacles for pollen employed by a particular species are not available, it may adopt those employed by others. Thus in a strong nest of *B. agrorum*, one of the pocket-making species that I had under observation in 1910, the workers, during a period when there were no growing larvæ and consequently no pockets for pollen, dropped all the pollen they brought home

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into a special waxen cell they had constructed, like *terrestris*, on the top of some cocoons. Also a colony of *B. hortorum*, another pocket-maker, being in an advanced stage, and having no growing larvæ, placed pollen in the cocoons vacated by the young queens, but only lined the interior of the cocoons with it."





In this connection the present writer would like to call attention to the fact that *Bremus americanorum* (cf. Franklin, '12/'13 p. 405) and *Bremus fervidus*, two of our American *Pocket*-

makers, not only store pollen under the conditions specified by Sladen ('12, p. 44), but that toward the end of the summer at the height of brood-rearing—prosperous colonies of these two species store considerable quantities of pollen, in some cases in shallow waxen bowls which are usually constructed near the periphery of the comb. (cf. Fig. 1). From these facts, it is evident that Sladen's ('99 and '12) term *Pollen-storers* is of little use in any comprehensive classification of the Bremidæ.

Furthermore, in regard to certain *Pocket-makers*, *e.g.*, *B. americanorum* and *B. fervidus*, it must be pointed out that the habit of making pockets is resorted to only in the case of those larvæ which are destined to become workers, while the brood which furnishes the other two castes (queens and males) is fed by regurgitation; *i.e.*, in the same manner as are those of the nonpocket-making species, a fact to which the writer has called attention in an earlier paper (cf. Plath '23a, p. 339). However, since this method of feeding the male and queen larvæ is not employed—at least in the temperate regions—until toward the end of the breeding season, and since the method by which these Bremidæ feed their worker brood is quite distinctive, it seems best to retain the term *Pocket-makers*, unless future investigations show that the use of this term is impracticable.

We now come to Sladen's ('12) division of the *Pocket-makers* into *Pollen-primers* and *Carder-bees*. As already mentioned, Sladen later ('12, pp. 274–275) removed two species from the *Pollen-primers*: but, as will be seen from the following observations, the term *Pollen-primers* will have to be completely rejected as a subdivision of the *Pocket-makers*.

In the fall of 1921 the present writer (cf. Plath '22a, p. 34 and '22b, p. 195) made detailed observations on a large colony of *Bremus impatiens*, a non-pocket-making species, and in this case the egg-cells were regularly primed with pollen pellets before the workers oviposited in them.⁴

Even more unsatisfactory is the term "Long-faced Humblebees" which Sladen ('12, p. 275) introduced later, since *Bremus mendax*, which structurally belongs to an entirely different group,

⁴ Incidentally this observation also shows that von Buttel-Reepen's ('03, p. 35) explanation of the pollen priming habit of bumblebees is incorrect (cf. also Sladen, '12, pp. 274-275).

and probably is a non-pocket-making species, has a longer face (cf. Krüger, '20, pp. 310 and 359) than either of the two species mentioned by Sladen ('12, p. 275).

Equally impracticable is the term *Carder-bees* which Sladen ('12, pp. 152–153) applies to the second subdivision of the *Pocket-makers*. The collecting of nesting material, the character on which Sladen ('12, p. 17) based this group, is more or less common to all species of the genus *Bremus*, including the non-pocket-making species. However, by the rejection of the term *Carder-bees*, the writer does not wish to imply that the species which Sladen ('12, p. 152) includes under this term do not constitute a distinct group.

Having pointed out the inadequacy of Sladen's ('12) classification as applied to some of our North American Bremidæ, the writer would suggest the following changes in Sladen's ('12) scheme. The name Marsipæa ⁵ (from Greek marsipos, a pouch, and poiein, to make) is proposed as a substitute for Sladen's ('12) term pocket-makers. This change would result in a suitable name for Sladen's pollen-storers (the non-pocket-making species) which could then be designated as the Amarsipæa. For reasons already stated, it is further suggested that the terms Pollen-primers, Long-faced humble-bees, and Carder-bees be droped as subdivisions of the Marsipæa.

Concerning two species belonging to the Amarsipæa, Sladen ('12, p. 36) says: "The larvæ of *B. terrestris* and *lucorum* do not keep together in a compact mass, but as they begin to grow large each one acquires its own covering of wax, although they do not separate completely; the cocoons, therefore, do not form definite clusters, and are easily detached from one another." And in the next paragraph he continues: "With most of the species the skin of wax that covers each batch of larvæ is to the unaided eye unbroken, but as the larvæ grow, *B. terrestris, lucorum, and latreillellus* leave visible holes in the wax, which, when the larvæ approach full size, become large. The larvæ would now run the risk of falling out of their soft wax covering, which would mean their destruction, for a naked larva is always carried out of the nest; but they avoid this danger by enclosing themselves in a

⁵ The writer here wishes to express his thanks to Professors W. G. Aurelio and W. M. Wheeler for their valuable suggestions concerning these terms.

loose web of silk, doing this a day or two before they begin to spin their cocoons."

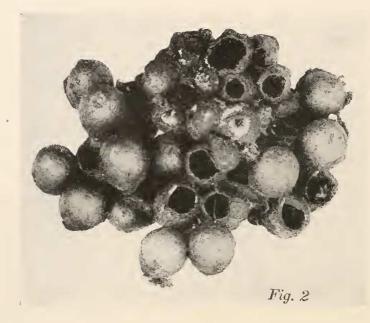


FIG. 2. Comb of Bremus affinis showing exposed larvæ. Natural size.

In this connection the writer would like to call attention to the fact that some of our American Amarsipæa, e.g., Bremus affinis, occidentalis, and terricola, have the same habit (cf. Fig. 2). Quite contrary to this treatment of the larvæ is that of the other American and European Amarsipæa whose habits have been studied, for the latter carefully keep their larvæ covered with wax (cf. Fig. 3).

Because of this difference in habit, the present writer proposes the name *Phaneroschadonenta* (from Greek *phaneros*, visible, and *schadon*, a bee larva) for those *Amarsipæa* whose larvæ are visible during the greater part of their development, and the name *Cryptoschadonenta* (from Greek *cryptos*, hidden) for those *Amarsipæa* which keep their larvæ covered with wax.

In addition to the very loosely connected cocoons and the uncovered larvæ, the *Phaneroschadonenta* exhibit a number of other peculiarities which mark them as a distinct group. Among

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these may be mentioned (1) the short antennæ of the males, (2) the similarity in form between males and workers, and (3) the extreme shortness of the head.⁶ This last character is coupled

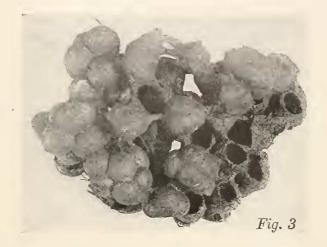


FIG. 3. Comb of *Bremus impatiens*, a typical example of the *Cryptoschadonenta*. Natural size.

with a short tongue, which makes it necessary for this group of bumblebees to perforate long-tubed flowers in order to secure the nectar. Because of this habit they have been given the name *Disteleologists* (cf. Haeckel, '66; Müller, '79; and von Buttel-Reepen, '14), a subject which the writer intends to discuss in another paper.

The *Phaneroschadonenta* also have the following interesting characteristics: (I) they construct—usually near the center of the comb—one or more bulky, waxen tubes in which they store large quantities of pollen (cf. Figs. 4 and 5); (2) the wax which they produce is unusually dark and brittle, as if mixed with black soil; and (3) their males, like those of the genus *Psithyrus*, are rather sluggish as compared with those of other species.⁷ The writer would here also like to point out that the *Phaneroschadonenta* appear early in the spring, that they do not nest on

⁶ Cf. Radowszkowski ('84), Friese and von Wagner ('10), Vogt ('11), Franklin ('12/'13), and Krüger ('20).

 $^{^7}$ Cf. Schmiedeknecht ('78), Hoffer ('82, '82/'83), Saunders ('09), Sladen ('12), and Frison ('17).

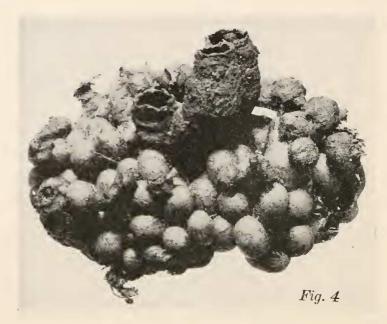


FIG. 4. Comb of Bremus affinis showing three pollen cylinders. Natural siz e

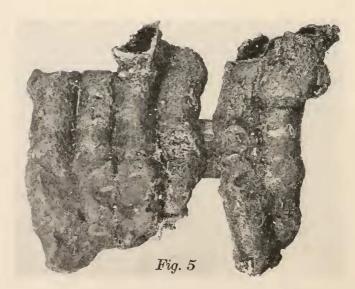


FIG. 5. Six pollen cylinders taken from a nest of *Bremus affinis*. Natural siz Sometimes more than a dozen of these pollen cylinders are found in one nest.

the surface of the ground, and that—as far as known—they do not occur in South America.

However, it may be necessary to use the terms *Phanero-* and *Cryptoschadonenta* only provisionally, since Sladen ('12, pp. 36-37 and 185) states that *Bremus latreillellus*, a *pocket-maker (Marsipæa*), also leaves its larvæ uncovered. This seems strange, since the other *Marsipæa* studied are very solicitous to keep their larvæ completely covered with wax (cf. Fig. 6), and this fact



FIG. 6. Comb of *Bremus americanorum* showing (a) three pockets, and (b) worker larvæ completely enclosed by wax. Natural size.

suggests the possibility that Sladen's ('12) observations on *Bremus latreillellus* may have been made during extremely hot weather, when, due to the softening of the wax, all bumblebee larvæ are likely to become exposed. Should subsequent observations confirm Sladen's ('12, pp. 37 and 185) statement concerning *Bremus latreillellus*, other terms will have to be substituted for *Phanero*-and *Cryptoschadonenta* to bring out the distinctness of this group of bumblebees.

The various American and European species of bumblebees whose methods of rearing their young have been studied up to

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the present are listed in Table I. with the suggested modifications of Sladen's ('99 and '12) scheme.

TABLE I.

AMARSIPŒA. Phaneroschadonenta.

1. 2. 3.	Bremus 	affinis occidentalis terricola	American Species.
4.		lucorum ⁸	European
5.	6.6	terrestris 8	Species
			Construction
			Cryptoschadonen
6.	Bremus	bimaculatus	
7.	* *	impatiens	
8.	* *	perplexus	American
9.	* *	ternarius	Species.
10,	6 6	vagans	Species.
11.	* *	auricomus ⁹	
12.	* *	separatus	J
13.	4.6	jonellus 8	
14.	6.6	lapidarius ⁸	European
15.	4.6	lapponicus 8	Species.
16.	* *	pratorum ⁸) •
			Marsipæa.
17.	Bremus	americanorum	American
18.	6.6	fervidus	Species.
		1	
19.	4.6	hortorum ⁸	
20.	**	ruderatus ⁸	European Species.
2I. 22.	**	distinguendus ⁸ latreillellus ⁸	
22.	4.6	agrorum ⁸	
23.	6.6	derhamellus ⁸	
25.	**	helferanus 8	
26.	**	muscorum ⁸	
27.	6.6	sylvarum ⁸	
		-	/

Concerning the relative temper of the Marsi- and Amarsipæa, Sladen ('99, pp. 230-231) says: "It will be noticed that the *pouch-makers* include roughly the timid species. The *pollenstorers*, on the contrary, consist of the bolder species." This is not true of our New England Marsipæa, e.g., Bremus americanorum and Bremus fervidus, these being the most vicious

⁸ According to Sladen ('12, pp. 152-153).

9 According to Frison ('17, pp. 284).

bumblebee species with which the present writer has come in contact, while most of our *Amarsipwa* are comparatively gentle.

It will be interesting to see whether the various bumblebee groups which have been established on the basis of structure are really homogeneous species, when their habits are studied from a taxonomic viewpoint. In the light of our present knowledge, we should expect the seven American groups (cf. Franklin, '12/ '13) of the genus *Bremus* to belong to the biological subdivisions as indicated in Table II.

TABLE II.

AMARSIPŒA. Phaneroschadonenta.

1. Terrestris group.

Cryptoschadonenta.

MARSIPEA.

2. Auricomus group.¹⁰

3. Fraternus group.¹⁰

4. Kirbyellus group.¹¹

5. Pratorum group.

6. Borealis group. 11

7. Dumoucheli group.

If Krüger's ('16 and '20) subdivision of the Bremidæ into two sections is really as far-reaching as it appears to be, we should expect the members of the *Borealis* group to belong to the *Mar*sipæa, and those of the *Kirbyellus* group to the *Amarsipæa*, since the spine is present in the former, but absent in the latter.

It will also be interesting to investigate the methods which the Bremidæ employ in feeding the larvæ of the genus *Psithyrus*, since certain species of the latter, *e.g.*, *Psithyrus variabilis*, breed in the nests of the *Marsipæa*, while others, *e.g.*. *Psithyrus ashtoni*, are parasitic on the *Amarsipæa*.

Due to a lack of sufficient material, the writer has been unable to determine whether the species for which Robertson ('03) erected the genus *Bombias* have any clearly defined biological peculiarities ¹² which would serve as suitable biological characters for distinguishing this group.

¹⁰ Belonging to the genus Bombias of Robertson ('03).

¹¹ Probably.

¹² The males of this group, like those of closely related European species, have their own peculiar habits (cf. Schmiedeknecht, '78; Hoffer, '82/'83; Robertson,

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SUMMARY.

1. Contrary to the assertions of Wagner ('06), biological characters are of considerable importance in determining the relationships between the various species of bumblebees, while structural characters frequently make it possible to draw inferences as to the habits of these insects.

2. Our North American Marsipæa—at least Bremus americanorum and Bremus fervidus—feed only their worker brood through pockets, while those larvæ which are destined to become queens and males are fed by regurgitation.

3. The use of the terms *Pollen-primers*, *Carder-bees*, and *Long-faced humble-bees* (cf. Sladen '12) is impracticable in any comprehensive classification of the Bremidæ.

4. Von Buttel-Reepen's ('03) explanation of the pollen-priming habit of bumblebees is not substantiated by the biology of some of our North American species.

LITERATURE CITED.

Ball, F. J.

- '14 Les Bourdons de la Belgique. Ann. Soc. Ent. Belg., Vol. 58, pp. 77-108, Pl. I.
- Buttel-Reepen, H. v.
 - '03 Die stammesgeschichtliche Entstehung des Bienenstaates, sowie Beiträge zur Lebensweise der solitären und sozialen Bienen (Hummeln, Meliponen, etc.). Georg Thieme, Leipzig.
 - '07 Zur Psychobiologie der Hummeln. I. Biol. Centralbl., Vol. 27, pp. 579-613.
 - '14 Dysteleologen in der Natur. (Zur Psychobiologie der Hummeln II.). Biol. Centralbl., Vol. 34, pp. 664–684.
- Dalla Torre, K. W. v.
 - '82 Bemerkungen zur Gattung Bombus Latr. Ber. naturw.-med. Ver. Innsbruck, Vol. 12, pp. 14-31.

Franklin, H. J.

'12/'13 The Bombidæ of the New World. Trans. Amer. Ent. Soc., Vol. 38, pp. 177-486, Vol. 39, pp. 73-200, Pls. 1-22.

Friese, H. und Wagner, F. v.

'10 Zoologische Studien an Hummeln. I. Die Hummeln der deutschen Fauna. Zool. Jahrb., Abt. Syst., Vol. 29, pp. 1–104, Pls. 1–7. 20 figs,

Frison, T. H.

'17 Notes on Bombidæ, and on the Life History of *Bombus auricomus* Robt. Ann. Ent. Soc. Amer., Vol. 10, pp. 277–286, Pls. 23 and 24.

'03; Saunders, '09; Sladen, '12; and Frison, '17); however it seems desirable to look for additional biological characters before separating this group from the other $Amarsip \alpha a$.

'23 Systematic and Biological Notes on Bumblebees (Bremidæ; Hymenoptera). Trans. Am. Ent. Soc., Vol. 48, pp. 307-326.

Haeckel, E.

'66 Dysteleologie oder Unzweckmässigkeitslehre. Generclle Morphologie der Organismen, Vol. 2, pp. 266–285. Georg Reimer, Berlin.

Hoffer, E.

- '82 Die Hummelbauten. Kosmos, Vol. 12, pp. 412-421.
- '82/'83 Die Hummeln Steiermarks. Lebensgeschichte und Beschreibung derselben. Leuschner & Lubensky, Graz.

Krüger, E.

- '16 Untersuchungen zur natürlichen Verwandtschaft der Hummeln. Verh. Naturw. Ver. Hamburg, (3) Vol. 23, p. lxxxvi.
- '20 Beiträge zur Systematik und Morphologie der mittel-europäischen Hummeln. Zool. Jahrb., Abt. Syst., Vol. 42, pp. 289-464, Pls. 3-7, 8 figs.

Müller, H.

'79 Bombus mastrucatus, ein Dysteleolog unter den alpinen Blumenbesuchern. Kosmos, Vol. 5, pp. 422-431.

Plath, O. E.

- ²²² Notes on *Psithyrus*, with Records of Two New American Hosts. BIOL. BULL., Vol. 43, pp. 23-44, Pl. I.
- '22b Notes on the Nesting Habits of Several North American Bumblebees. Psyche, Vol. 29, pp. 189–202.
- ¹23*a* Breeding Experiments with Confined *Bremus* (*Bombus*) Queens. BIOL. BULL., Vol. 45, pp. 325-341.
- ¹23*b* Notes on the Egg-eating Habit of Bumblebees. Psyche, Vol. 30, pp. 193–202.
- '24 Miscellaneous Biological Observations on Bumblebees. BIOL. BULL., Vol. 47, pp. 65-78, 2 figs.

Radowzkowski, O.

'84 Révision des armures copulatrices des males du genre Bombus, Bull. Soc. Nat. Moscou, Vol. 59, pp. 50–92, Pls. 1–4.

Robertson, C.

'03 Synopsis of Megachilidæ and Bombinæ. Trans. Amer. Ent. Soc., Vol. 29, pp. 163-178.

Saunders, E.

'09 Bombi and other Aculeates Collected in 1908 in the Berner Oberland by the Rev. A. E. Eaton, M.A. Ent. Monthl. Mag., Ser. 2, Vol. 20 (Vol. 45), pp. 83-84.

Schmiedeknecht, O.

'78 Monographie der in Thüringen vorkommenden Arten der Hymenopteren-Gattung Bombus. Jenaische Zeitschr. Naturw., Vol. 12, pp. 303-430, Pls. 10 and 11.

Sladen, F. W. L.

- '99 Bombi in Captivity, and Habits of Psithyrus. Ent. Monthl. Mag., Vol. 35, pp. 230-234.
- '12 The Humble-bee, its Life-History and How to Domesticate It. Macmillan & Co., London.

Smith, F.

'76 Catalogue of British Hymenoptera in the Collection of the British Museum London.

Vogt, O.

'II Studien über das Artproblem. 2. Mitteilung. Über das Variieren der Hummeln. 2. Teil. (Schluss). Sitzungsber. Gesellsch. naturforsch. Freunde, pp. 31-74.

Wagner, W.

'06/'07 Psycho-biologische Untersuchungen an Hummeln mit Bezugnahme auf die Frage der Geselligkeit im Tierreiche. Zoologica, Vol. 19, pp. 1-239, Pl. 1, 136 figs.

Wheeler, W. M.

'19 The Phoresy of Antherophagus. Psyche, Vol. 26, pp. 145-152, 1 fig.